What the Immaculate Pigeon Teaches the Burdened Mind

To support his theory, Darwin studied the rock dove and its descendants

by Stephen Jay Gould

Two successive symbols of Saint Louis typify the passages of our century. Saarinen's magnificent arch, gleaming and immaculate, seems to soar from the Mississippi River into heaven (an optical illusion, in large part, cleverly produced by a gradual decrease in edge length from fifty-four feet at the base of the structure to seventeen feet at the summit. Our minds work on the expectation of a constant size, and the marked decrease therefore makes the summit seem ever so much higher than its actual 630 feet—the size of an ordinary skyscraper in a modern city). By contrast, Saint Louis's older symbol, an equestrian statue of the eponymous Louis IX, the only canonized king of France, still stands in front of the Art Museum in Forest Park. It is anything but immaculate, thanks to that primary spotting agent of all cities—pigeons.

As a team, pigeons and the statue of Saint Louis go way back. The current statue is a 1906 recasting in bronze of the impermanent original made for the main entrance to one of the world's greatest expositions—the 1904 World's Fair, held to celebrate (if just a bit late) the centenary of the Louisiana Purchase. The Fair must have been spectacular; my wife's family, raised in Saint Louis, still mentions it with awe in stories passed down through three generations. The Fair gave us iced tea, ice cream cones, and a great song, "Meet Me in Saint Louis, Louis" (many folks don't even know the next line, "Meet me at the Fair").

A Ferris wheel stood twenty-five stories high; Scott Joplin played his rags. The Pike, main street of the amusement area, featured daily reenactments of the Boer War and the Galveston Flood. The world's greatest athletes came to participate in the third Olympic Games. The fairgrounds, bathed at night in the newfangled invention of electric lighting, inspired Henry Adams to write:

> The world has never witnessed so marvelous a phantasm; by night Arabia's crimson sands had never returned a glow half so astonishing [a statement that will need revision after the night bombing of our Desert Storm], as one wandered among long lines of white palaces, exquisitely lighted by thousands and thousands of electric candles, soft, rich, shadowy, palpable in their sensuous depths [from *The Education of Henry Adams*].

This statement also makes sense of the next two lines of the famous song: "Don't tell me the lights are shining / Any place but there."

Intellectuals must be constantly clever and industrious. We know that we are peripheral to society's main thrust, and we must be constantly vigilant in seeking opportunities to piggyback on larger enterprises—to find something so big and so expensive that prevailing powers will grant us a bit of space and attention at the edges. The hoopla and funding of major exhibitions often give us a little room for a smaller celebration in our own style. I was invited to give a speech at something called the Academic Olympiad in Seoul during the last great athletic show. (I wasn't able to go and never heard boo about the outcome—although television deluged us with all the details about javelins and the hop, step, and jump.) Similarly, as the 1904 World's Fair led to the establishment of Washington University, academicians rallied to hold a Congress of Arts and Science at the Universal Exposition (as the Fair was officially called). At this convocation, the great American biologist Charles Otis Whitman gave a leading address with the general title: "The Problem of the Origin of Species." He spoke primarily about pigeons.

Whitman's work, while treating so humble a subject, had a certain panache and boldness. He wrote at a time when biologists, although fully confident about the fact of evolution, had become very confused and polemical about the causes of evolutionary change. Darwin's own theory of natural selection had never commanded majority support (and would not emerge as a consensus until the 1930s). As visitors ate their first ice cream cones on the Pike, at least three other theories of evolutionary change enjoyed strong support among biologists: (1) the inheritance of acquired characters, or "Lamarckism"; (2) the origin of species in sudden jumps of genetic change, or "mutationism"; (3) the unfolding of evolution along limited pathways set by the genetic and developmental programs of organisms, or "orthogenesis" (literally, "straight line generation"). Whitman, who had been raising and breeding pigeons for decades, defended the last alternative, orthogenesis, and thereby relegated Darwinian natural selection to a small and subsidiary role in evolution.

Whitman's boldness did not lie in his choice of the orthogenetic theory, for this argument was a strong contender in his day, although probably the least popular of the three major alternatives to Darwinism. We judge a man intrepid when he uses his adversary's tools or data to support a rival system. A famous story about Ty Cobb tells of his disgust with Babe

Ruth's new style of power hitting (Ruth swatted more home runs per year all by himself than most teams had managed in a season during earlier times). Cobb, the greatest and most artful practitioner of the earlier style of slap, hit, and scramble for a run at a time, held his hands apart on the bat, slipped them together high on the bat as the pitch came in (thus achieving maximal control while sacrificing power), and then slapped the ball to his chosen spot. Ruth, by contrast (and following the strategy of all sluggers), held the bat at the end and swung away, missing far more often than he connected. Cobb regarded this style as easy and vulgar, however effective. One day near the end of his career, and to show his contempt in the most public way, Cobb ostentatiously held the bat in Ruth's manner, hit three home runs in a single game, and then went right back to his older, favored style forever after.

Whitman's assault on Darwin's theory from within was far bolder and more sustained, if not quite so showy. For Whitman had chosen, for study over decades, the very organisms—pigeons—that Darwin had selected as the primary empirical support for his own theory.

Darwin stated in chapter one of the *Origin of Species:*

> Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons. I have kept every breed which I could purchase, or obtain, and have been most kindly favored with skins from several quarters of the world.... I have associated with several eminent fanciers, and have been permitted to join two of the London Pigeon Clubs.

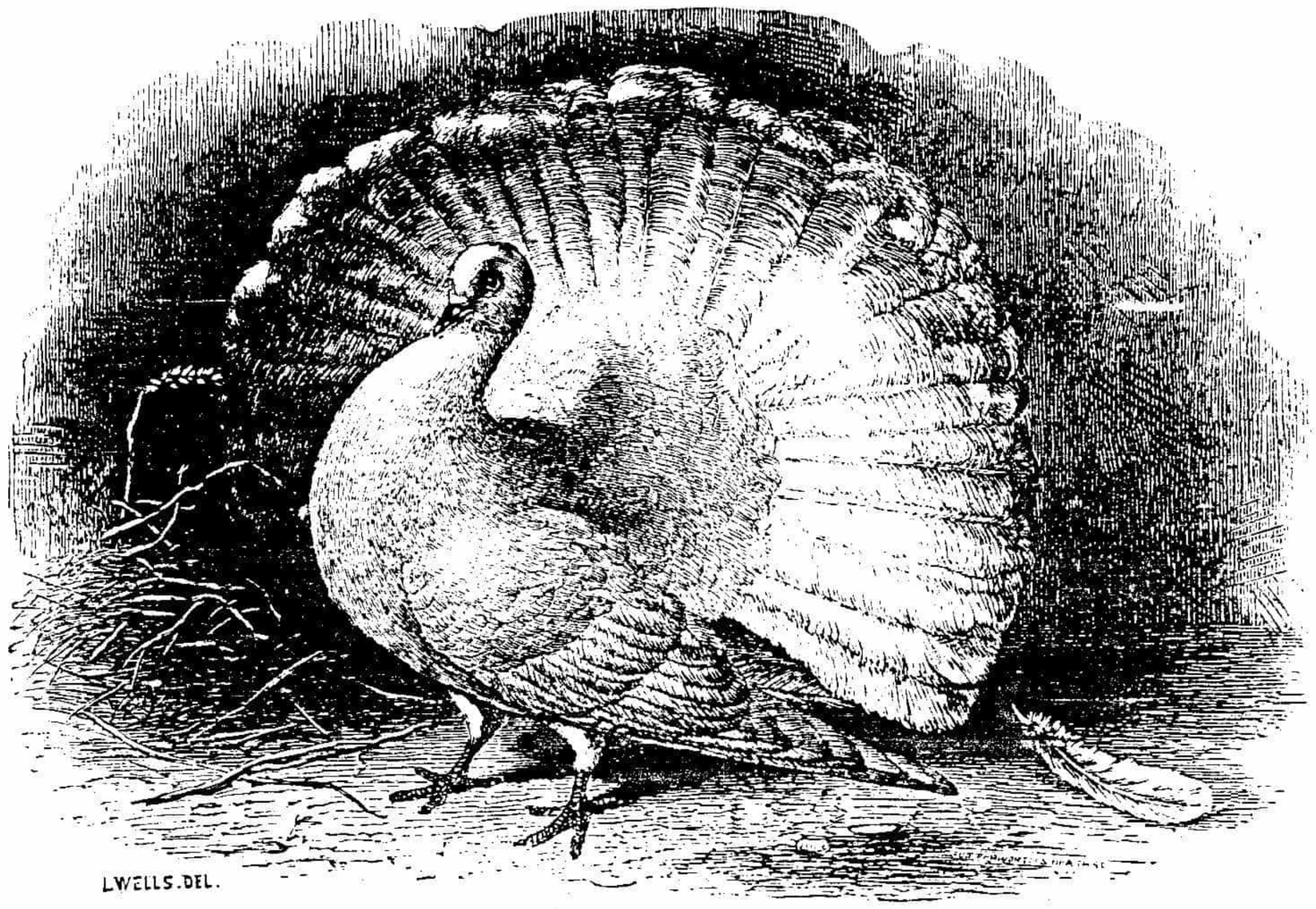
Darwin stated an excellent reason for his choice in the next sentence:

> The diversity of the breeds is something astonishing. Compare the English carrier and the short-faced tumbler, and see the wonderful difference in their beaks.... The common tumbler has the singular and strictly inherited habit of flying at a great height in a compact flock, and tumbling in the air head over heels.... The Jacobin has the feathers so much reversed along the back of the neck that they form a hood.... The fantail has thirty or even forty tail-feathers, instead of twelve or fourteen, the normal number in all members of the great pigeon family; and these feathers are kept expanded, and are carried so erect that in good birds the head and tail touch.

These breeds are so different that any specialist, if "he were told that they were wild birds," would assume major taxonomic distinctions based upon substantial differences. "I do not believe," Darwin wrote, "that any ornithologist would place the English carrier, the short-faced tumbler, the runt, the barb, pouter, and fantail in the same genus."

And yet, demonstrably by their interbreeding and their known history, all these pigeons belong to the same species and therefore have a common evolutionary source—the rock pigeon, *Columba livia.* Darwin wrote: "Great as the differences are between the breeds of pigeons, I am fully convinced that the common opinion of naturalists is correct, namely, that all have descended from the rock-pigeon (*Columba livia*)." (Darwin might have chosen the even more familiar example of dogs to make the same point, but he was not convinced that all dog breeds came from a common wolf source, whereas the evidence for a single progenitor of all pigeons seemed incontrovertible.) Only one step—the key analogical argument that powers the entire *Origin of Species*—remained to secure the most important argument in the history of biology and to make pigeons the heroes of reform: if human breeding of pigeons could produce, in a few thousand years at most, differences apparently as great as those separating genera, then why deny to a vastly more potent nature, working over millions of years, the power to construct the entire history of life by evolution? Why acknowledge the plain fact of evolution among pigeons and then insist that all natural species, many no more different one from the other than pigeon breeds, were created by God in their permanent form?

Whitman, of course, did not disagree with Darwin's focal contention that pigeons had evolved, but he strongly questioned Darwin's opinion on *how* they and other species had arisen. Charles Otis Whitman (1842–1910), although scarcely a household name today, was the leading American biologist of his generation. He was, perhaps, the last great thinker to span the transition from the pre-Darwinian world to the rise of twentieth-century experimental traditions—for he had studied with Louis Agassiz, the last true creationist of real stature, and he lived to found and direct the symbol of modernism in American biology, the Marine Biological Laboratory at Woods Hole. In his research, Whitman was best known for meticulous work on "cell lineage" studies in embryology—tracing the eventual fate of the first few embryonic cells in forming various parts of the body. In promoting this form of research as canonical in Woods Hole, and in establishing at his new laboratory the finest young American biologists, Whitman succeeded in bringing to this country the experimental and mechanistic traditions championed as the soul of "modernism" in Europe.



Darwin included this illustration of the "showiest" pigeon breed, the English fantail, in his book The Variation of Animals and Plants under Domestication.
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In this light, I have always had trouble remembering that Whitman's main love in research lay in the opposite camp of "old-fashioned" and largely descriptive natural history—decades of work on the raising, breeding, and observation of pigeons. This passion even led to his death. In Chicago (where he served as professor of biology at the university), on the first chill day of December 1910, Whitman worked all afternoon in his backyard, hastily preparing winter quarters for his pigeons to save them from the cold. As a result, he developed pneumonia and died five days later. F. R. Lillie, once his assistant and then his successor at Woods Hole, eulogized his old boss: "In his zeal for his pigeons, he forgot himself."

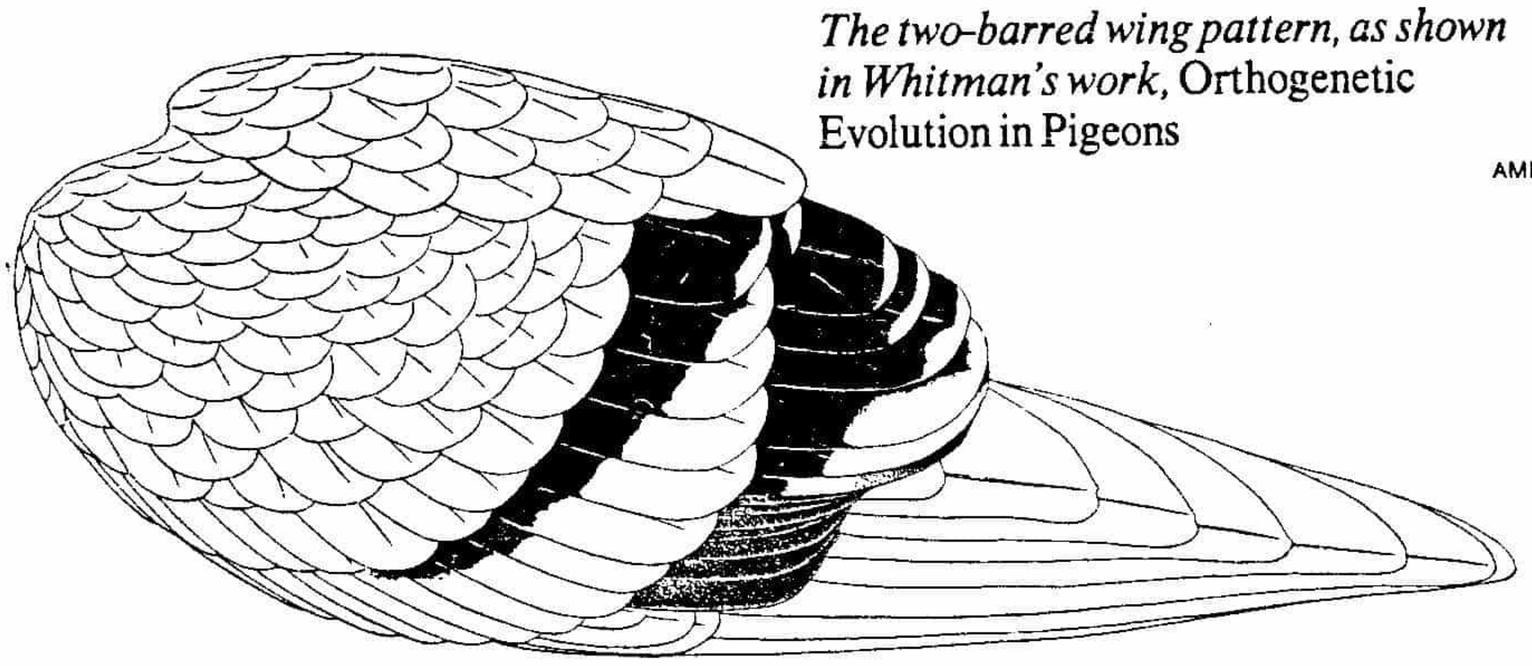
Unfortunately, Whitman died before completing and integrating his lifelong work on pigeons. He had published a few preliminary addresses (most notably, his offering in Saint Louis), but never the promised major statement. I can't help thinking that the history of evolutionary thought might have been different had Whitman lived to promulgate and proselytize his non-Darwinian evolutionary ideas. His colleagues did gather his notes and data into a three-volume posthumous work on pigeons, which finally appeared in 1919. But this work (the basis of my essay) was too disjointed, too incomplete, and above all, too late to win its potential influence.

Darwin's pigeon agenda had been wider than the simple demonstration of evolution. He also wished to promote his own theory about how evolution had occurred—natural selection. Again, he relied on argument by analogy: pigeon breeds had been made by artificial selection based on human preferences for gaudiness (pouters, fantails) or utility (carriers, racers).

> When a bird presenting some conspicuous variation has been preserved, and its offspring have been selected, carefully matched, and again propagated, and so onwards during successive generations, the principle is so obvious that nothing more need be said about it. [This quotation comes from Darwin's most extensive discussion of pigeons, two long chapters in his 1868 book, *The Variation of Animals and Plants under Domestication.* Other statements are cited from the *Origin of Species,* 1859.] May not those naturalists who . . . admit that many of our domestic races have descended from the same parents—may they not learn a lesson of caution, when they deride the idea of species in a state of nature being lineal descendants of other species?

Orthogeneticists like Whitman did not deny natural selection but viewed Darwin's force as too weak to accomplish anything but a bit of superficial tinkering. Natural selection, they argued, can make nothing, and can only accept or reject the variation that arises naturally among differing organisms in an interbreeding population. If the genetic and embryological systems of organisms prescribe a definite direction to this variability, then natural selection is rendered powerless to set the course of evolutionary change. Suppose, for example, that size in offspring only varied in a single direction from parental dimensions; that is, all kids ended up either the same size or taller than their folks. What could natural selection do? Darwin's force could hasten an inherent trend by favoring the taller offspring. At most, selection could prevent a trend, and keep the population stable, by eliminating the taller offspring and preserving only those of parental dimensions. But selection could not work counter to the inherent direction of variation because no raw material would be available for trends in any direction other than increasing size. Thus, selection would be a force subsidiary to the internal tendency for directional variation, or orthogenesis.

Darwin, of course, was aware of the logic of this destructive argument. He



The two-barred wing pattern, as shown in Whitman's work, Orthogenetic Evolution in Pigeons

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countered by claiming that variation has no inherent direction and occurs "at random" relative to the favored path of natural selection. (This is the context for Darwin's confusing claim that variation is random—a statement that has led many people into the worst vernacular misconception about Darwinism: the false belief that Darwin viewed evolutionary change itself as random, and that the manifest order of life therefore disproves his theory. In Darwin's scheme, variation is random, but natural selection is a deterministic force, adapting organisms to changes in their local environments. In fact, Darwin made his claim about the randomness of variation in order to empower natural selection as a directional agent.) If variation is only random raw material, occurring in no favored direction relative to environmental advantages, then some other force must shape this formless potential into adaptive change. Random raw material needs another force to carve out and preserve the advantageous portion—and natural selection plays this role in Darwin's system. But orthogenetically directed variation requires no other shaping force and can set an evolutionary trend all by itself.

Whitman therefore set out to prove that an inherent trend in variation pervades the pigeon lineage—a trend too powerful for natural selection to alter in direction or even to slow substantially. Whitman based his argument on the bird's patterns of coloration.

The feral pigeons that speckle our public statuary show two basic color patterns in their extensive repertoire of variation. Some have two black bars on the front edges of their wings and a uniform gray color elsewhere; others develop black splotches, called checkers, on some or all wing feathers, but also retain the two bars (although usually in more indistinct form). The bars, in any case, are composed of checkers (on several adjacent feathers) that line up to produce the impression of a broad, continuous stripe.

Darwin had assumed that ancestral pigeons were two-barred and that checkers represented an evolved modification by intensification of coloration. Whitman reversed Darwin's perspective:

> The latter [two-barred] was regarded by Darwin as the typical wing pattern for *Columba livia*; the former [checkered] was supposed to be a variation arising therefrom, a frequent occurrence but of no importance. Just the contrary is true; the checkered pigeon represents the more ancient type, from which the two-barred type has been derived.

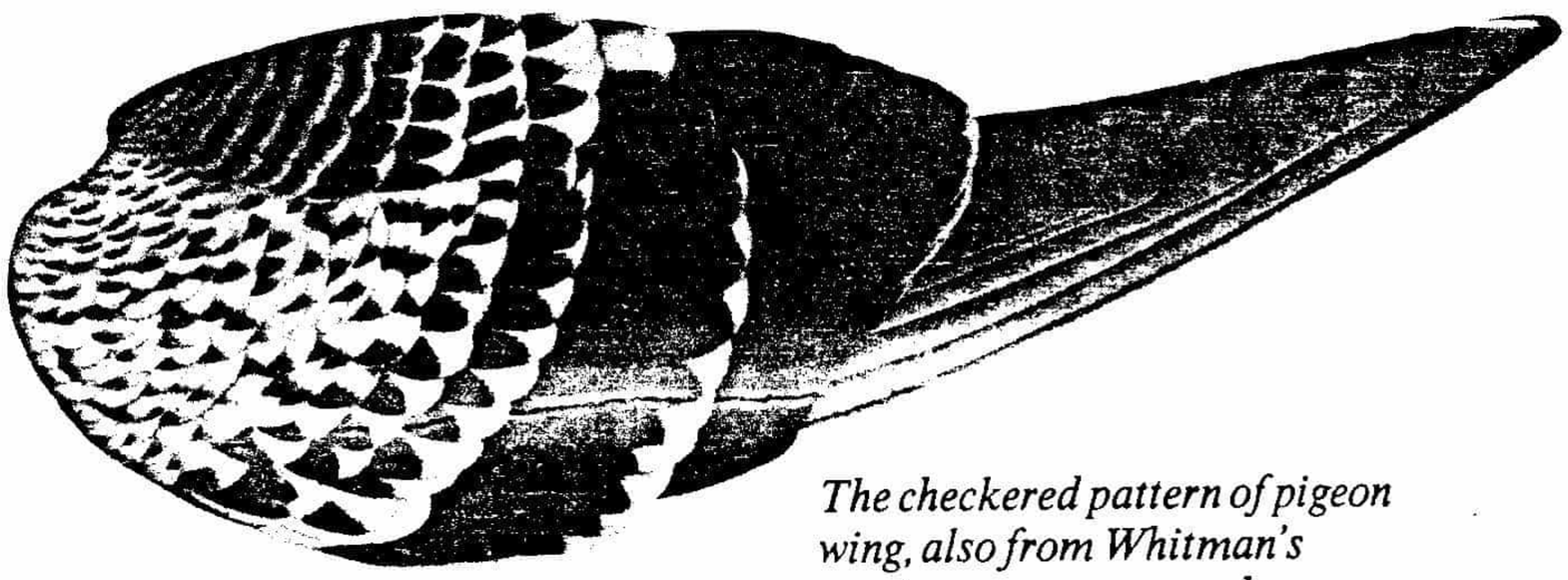
This reversal is of no great significance in itself, unless you happen to be a pigeon fancier devoted to the peculiarities of these generally unloved creatures. But Whitman made much of his inversion because his favored sequence of checkers-to-bars formed the major part of his proposed (and inexorable) orthogenetic sequence of internally prescribed variation—an evolutionary pattern inherent in the biological organization of pigeons and quite beyond the power of natural selection to deflect. The orthogenetic trend, Whitman argued, moved from original diffusion to later concentration of color. Checkers plus indistinct bars must come before clear bars and no checkers. In the lines following the quotation just cited, Whitman wrote:

> The direction of evolution in pattern in the rock pigeons has been from a condition of relative uniformity to one of regional differentiation.

But Whitman had an even bolder vision, based on the same orthogenetic pattern. Checkers-to-bars was no circumscribed peculiarity of domestic pigeons but only part of a much more extensive orthogenetic trend that pervaded the entire pigeon family (including all other species from mourning dove to passenger pigeon, which became extinct in the decade between Whitman's death and the posthumous publication of his monograph), and perhaps even all coloration in birds—an inherent and ineluctable progression from an original homogeneous checkering on all feathers, to the concentration of color in certain areas (checkers plus bars, and then to bars alone), to the reduction and weakening of these concentrations, to the final elimination of all color. Whitman located the ancestral state in the uniform checkering of some species—the "turtle dove pattern" in his terminology—and the final goal in some idealized, albinized version of the Holy Ghost, depicted as a pure white dove in so many medieval paintings. In short, and in his words, from uniform spotting to "immaculate monochrome," a most unpigeonlike state (in both appearance and deed), at least in our metaphors (also the quotation that piqued my interest, inspired this essay, and cast my initial thoughts toward Saint Louis). In a remarkable vision of inexorable movement through the entire great family of pigeons, Whitman wrote:

> When we look around among allied species and see the same bars reduced to about half dimensions in the rock pigeon of Manchuria, reduced to mere remnants of two to six spots in the stock dove, carried to complete obsoletion [*sic*] or to a few shadowy reminiscences in . . . *Columba rufina* of Brasil, gone past return in some of our domestic breeds and in many of the wild [doves and pigeons]—when we see all these stages multiplied and varied through some 400 to 500 wild species and 100 to 200 domestic breeds, and in general tending to the same goal, we begin to realize that they are . . . slowly passing phases in the progress of an orthogenetic process of evolution, which seems to have no fixed goal this side of an immaculate monochrome—possibly none short of complete albinism.

Moreover, while the progress of the



The checkered pattern of pigeon wing, also from Whitman's posthumous monograph

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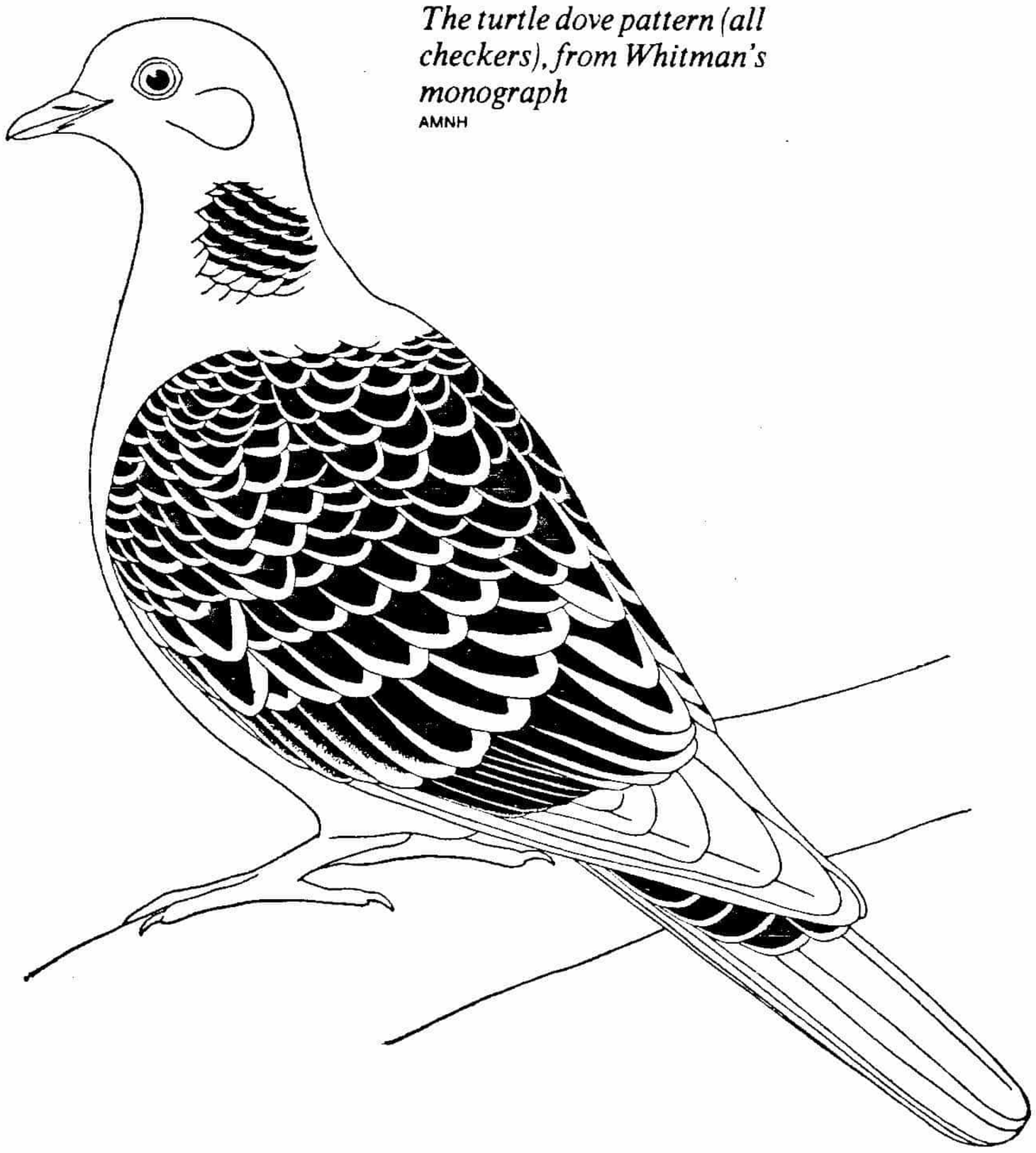

The turtle dove pattern (all checkers), from Whitman's monograph
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trend may be "lengthened or shortened, strengthened or weakened" by such subsidiary forces as natural selection, the orthogenetic sequence is invariable:

> The steps are seriated in a causal, genetic order—an order that admits no transpositions, no reversals, no mutational skips, no unpredictable chance intrusions.

When we discern the proper sequence of orthogenetic stages, evolution may become a predictive science: "Not only is the direction of the change hitherto discoverable, but its future course is predictable."

I have not resurrected Whitman's largely forgotten work in order to defend orthogenesis as a replacement for natural selection, for this is truly a dead issue decided long ago in Darwin's favor. Rather, from my deep admiration of Whitman's keen intelligence and my abiding respect for his decades of careful work with pigeons, I do wish to point out that his conclusions were not foolish and that several aspects of his work would repay our close study, even today. Consider three points that might prompt sympathy and interest.

1. *The false charge of teleology.* The standard one-liners of evolution texts dismiss orthogenesis as a theistically inspired, last-gasp effort to salvage some form of inherent goal and purpose in Darwin's new world. In this canard, supporters of orthogenesis abandoned rationality itself to embrace for their explanation of life a woolly mysticism of "vital forces" and "inherent directions"—the very concepts that science had struggled to discard in field after field, from cosmology to physics to chemistry. Whitman has been viewed as a particularly sad example of this slippage and surrender, for he had been such a committed mechanist in his earlier embryological work.

This hurtful charge is not only wrong but entirely backward. Whitman and nearly all other prominent supporters of orthogenesis maintained as firm a commitment to mechanical causation (some today might argue too firm), and as strong an aversion to mystical or spiritual direction, as any contemporary in this late nineteenth century age of industrial order. In the opening paragraph of his 1919 monograph on pigeons, Whitman wrote:

> His [Darwin's] triumph has won for us a common height from which we see the whole world of living beings as well as all inorganic nature; phenomena of every order we now regard as expressions of natural causes. The supernatural has no longer a standing in science; it has vanished like a dream, and the halls consecrated to its thralldom of the intellect are becoming radiant with a more cheerful faith.

In fact, Whitman's orthogenesis arose from his mechanical perspective, not in opposition to his former life's work. The orthogenetic trend was not a mystical impulse from outside but a mechanistic drive from within, based upon admittedly unknown laws of genetics and embryology. His work on cell lineages had mapped the fate of earliest cells in the embryo and had indicated that the source of eventual organs could be specified even in the tiny and formless clump of initial cells. If embryos grew so predictably, why should evolutionary change be devoid of similar order? "I venture to assert," Whitman wrote,

> that variation is sometimes orderly and at other times rather disorderly, and that the one is just as free from teleology as the other. . . . If a designer sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the laws of development exclude some lines of variation and favor others, there is certainly nothing supernatural in this.

2. *Whitman's evidence.* Modern detractors who misconstrue orthogenesis as old-fashioned teleology often assume that its supporters could only have been working on hope and the flimsiest of supposed evidence. But Whitman spent decades gathering reams of fascinating data (not all properly interpreted in our view, but still full of interest). He marshaled three major sources of evidence to support his orthogenetic theory: breeding, comparative anatomy, and ontogeny (the growth of individual birds).

In breeding, he found that he could develop a two-barred race from checkered parents by selecting birds with the weakest checkers in each generation. But he could never produce checkered birds from two-barred progenitors. In comparative anatomy, he argued that species judged more ancestral on other criteria grew plumages of early stages in the orthogenetic series. In ontogeny, he found that juvenile plumage exhibited earlier stages than adult feathers (a juvenile bird might molt its checkered feathers and then grow a two-barred adult plumage). Most nineteenth-century biologists believed that "ontogeny recapitulates phylogeny"—a mouthful meaning that individuals, in their embryology and growth, tend to pass through stages representing adult forms of their ancestry. Juvenile plumage would therefore represent an ancestral condition. The law of recapitulation is wrong (see my book *Ontogeny and Phylogeny*), but you can't blame Whitman for accepting the consensus of his time.

3. *Channels versus one-way streets.*

Whitman viewed his series of orthogenetic stages as a forced pathway—a one-way street with pigeons as the cars. He was clearly wrong in this, and two major errors invalidate his form of orthogenesis. First, the cars can go in either direction: Whitman's series may carve a road into a complex landscape, but the traffic flows both ways. Pigeons can either gain or lose color. Second, I doubt that either the checkered or two-barred condition represents a primitive state for domestic pigeons. The ancestor of domestic races was a population, not an individual, and populations are variable. I suspect that the parental population included both checkered and two-barred birds within a spectrum of variation and that the spectrum represents the ancestral condition.

But think about Whitman's vision in a slightly modified form and we have an idea that is not only valid but also full of potential insight in correcting a major misconception and teaching a fundamental truth about evolution. Think of this one-way street as a channel instead—a favored pathway of evolutionary variation set by the inherited genetic and developmental programs of organisms.

Evolution does not move in predictable and preformed directions; organisms are not balls on the top of inclined planes. The inherited constitution of organisms surely sets limits of all kinds upon possibilities for variation and just as surely channels change along certain pathways.

If natural selection controlled evolution entirely, then no such limits and pathways would exist, and organisms would be like billiard balls, fully capable of moving in any direction and subject to any change in position induced by the pool cue of natural selection. But, to borrow an old metaphor from Darwin's brilliant cousin Francis Galton, suppose that organisms are polyhedrons rather than billiard balls, and that they can only move by flipping from one side (on which they now rest) to an adjacent facet. They may need a push from natural selection to move at all, but the direction of change is largely set by internal limitations and possibilities. If inherited genetic and developmental programs build the facets of Galton's polyhedron, then strong internal constraints upon evolutionary change must exist, and Whitman's insight is correct, so long as we convert his one-way streets into channels—that is, strong biases in the direction of variation available for evolutionary change. Moreover, Whitman probably identified the most important internal channel of all—the pathway of ontogeny, or the growth of individuals. Evolutionary change works most easily with a direction

already established in growth—lengthening a bit here, cutting out a stage or two there, changing the relative timing of development among organs and parts.

The greatest vernacular misconception of evolution views the process as an inexorable machine, working to produce optimal adaptations as best solutions to problems posed by local environments and unconstrained by the whims and past histories of organisms. For example, I have monitored the "Ask the *Boston Globe*" science query column for years and have never known it to answer an evolutionary question in any but an adaptationist way. One correspondent asked, "Why do we have two breasts?" and the paper answered by citing a theory that the "right" number of breasts (for optimal adaptation) is one more than the usual number of offspring, thus providing a margin of safety, but not so large a margin as to become a burden. Since human females almost always have but a single child, two is the right number of breasts by this argument rooted in natural selection. I couldn't help but laugh when I read this conclusion. I do grasp the logic, but surely the primary channel of our anatomical design—bilateral symmetry—has something to do with the solution. Most externalities come in twos on our bodies—eyes, nostrils, ears, arms, legs, and so on—and the reason cannot be singleton births. Isn't this prior channel of architecture more likely to be the primary reason for two breasts?

If the adaptationist vision were true, we might gain the comfort of seeing ourselves, and all other creatures, as quintessentially "right," at least for our local environments of natural selection. But evolution is the science of history and its influence. We come to our local environments with the baggage of eons; we are not machines newly constructed for our current realities. These historical baggages are expressed as the genetic and developmental channels that led Whitman too far, but that, properly interpreted as strong biases in variation rather than one-way streets of change, would give us a much richer view of evolution as a subtle balance between constraints of history and reshapings by natural selection.

The power of the channels is a key to understanding our bodies and our minds; we will never grasp the evolutionary contribution to our nature if we persist in the naïve view that natural selection builds best solutions. We can accept the idea more readily for our bodies; hernias and lower back pain are the price we pay for walking upright with bodies evolved for quadrupedal life and not optimally redesigned. But how much of the quirkiness and limitations of our modes of thinking might also record a structure evolved during eons for other uses and only recently developing the varied phenomena of higher consciousness, and its primary tool of expression in language? Why are we so bad at so many mental operations? Why do we seem so singularly unable to grasp probability? Why do we classify by the painfully inadequate technique of dichotomy? Why can we not even conceive of infinity and eternity? Is the limit of current cosmological thinking a defect of data or a property of mind that gives us no access to more fruitful kinds of answers?

I do not mean this list as a statement of despair about our mental midgetry. To recognize a potential limit is to think about tools of possible transcendence. Freedom, as Spinoza said, is the recognition of necessity. Let us return once again to the proper metaphor of channels and remember the finest statement in literature about emerging from ruts: "There is a tide in the affairs of men, which, taken at the flood, leads on to fortune."

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